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Predatory ability and abundance forecast the ecological impacts of two aquatic invasive species

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Abstract

Characterising interspecific interaction strengths, combined with population abundances of prey and their novel predators, is critical to develop predictive invasion ecology. This is especially true of aquatic invasive species, which can pose a significant threat to the structure and stability of the ecosystems to which they are introduced. Here, we investigated consumer-resource dynamics of two globally-established aquatic invasive species, European green crab (*Carcinus maenas*) and brown trout (*Salmo trutta*). We explored the mediating effect of prey density on predatory impact in these invaders relative to functionally analogous native rock crab (*Cancer irroratus*) and Atlantic salmon (*Salmo salar*), respectively, feeding on shared prey (*Mytilus* sp. and *Tenebrio molitor*, respectively). We subsequently combined feeding rates with each predator's regional abundance to forecast relative ecological impacts. All predators demonstrated potentially destabilising Type II functional responses towards prey, with native rock crab and invasive brown trout exhibiting greater *per capita* impacts relative to their trophic analogues. Functional Response Ratios (attack rates divided by handling times) were higher for both invasive species, reflecting greater overall *per capita* effects compared to natives. Impact projections that incorporated predator abundances with *per capita* effects predicted severe impacts by European green crabs. However, brown trout, despite possessing higher *per capita* effects than Atlantic salmon, are projected to have low impact owing to currently low abun-

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dances in the sampled watershed. Should brown trout density increase sixfold, we predict it would exert higher impact than Atlantic salmon. Such impact-forecasting metrics and methods are thus vital tools to assist in the determination of current and future adverse impacts associated with aquatic invasive species.

Keywords
Aquatic invasive species, consumption rate, feeding, freshwater, functional response, Functional Response Ratio, impact, invasion, marine, predation, Relative Impact Potential

Introduction

Invasive species exert measurable and often catastrophic changes in recipient communities (Ricciardi et al. 2013; Gallardo et al. 2016; Flood et al. 2020). As invasion rates continue to increase globally (Seebens et al. 2017), understanding and mitigating invasion impacts is pivotal. Freshwater and marine environments support diverse assemblages of non-indigenous species (Strayer 2010). Many such species have had demonstrable impacts on their recipient systems, with approximately one-fifth of the 100 world's worst invasive species found in aquatic habitats (Kulhanek et al. 2011). However, comparative trait analyses between native and non-indigenous species have focused primarily on terrestrial ecosystems (Leffler et al. 2014). Evaluating the impacts of aquatic invasive species is, therefore, paramount to manage their effects (Ojaveer et al. 2015). However, the inherent difficulty associated with quantifying invasive species' ecological impacts requires a more mechanistic approach that can also forecast ecological impacts with readily available data, based on *per capita* effects and abundances of the interacting species (Dick et al. 2014, 2017a).

Analysis of a predator's density-dependent consumption rates [i.e. its functional response (FR)] can provide insights into its *per capita* effect (Holling 1959). In addition, experimentally-derived estimates of invasive species' *per capita* effects relative to those of native analogues are useful tools to forecast the former's potential ecological impact (Dick et al. 2014). Invasive species often demonstrate higher and more efficient resource utilisation relative to ecologically similar native species across taxonomic groups (Dick et al. 2014; Crookes et al. 2019; Dickey et al. 2021). Taking such *per capita* impact prediction one step further, the Functional Response Ratio (FRR) is derived from the FR's constituent parameters (attack rate divided by handling time). By synthesising its parameters into a single metric, the FRR provides greater mechanistic insight into drivers of predator impact on affected prey species than use of either attack rate or handling time variables in isolation (Cuthbert et al. 2019). As the FRR integrates predator effects at both low and high prey densities, it may provide increased predictive power of *per capita* type (i.e. FR) experiments (Cuthbert et al. 2019; Madzivanzira et al. 2021).

While species' resource consumption can provide insights into their projected ecological impacts (Dick et al. 2014), the magnitude of an effect is also determined by the predator's local abundance (Parker et al. 1999). Dick et al. (2017a) thus devised a new metric, the Relative Impact Potential (RIP), that incorporates *per capita* feeding rates

and local field abundances as proxies for functional and numerical responses, respectively, to predict the ecological impact of an invasive species versus that of a comparative native species. This method shows promise to screen potential invasive species and perform rapid impact assessments of established (as well as potential) invaders on both prey communities and relative to co-occurring native predators (Hoxha et al. 2018; DeRoy et al. 2020; Dickey et al. 2020a). Indeed, the RIP metric was 100% successful in its ability to predict the actual field impacts of a range of invasives across trophic and taxonomic groups (Dick et al. 2017a).

The objective of our study was to discern whether *per capita* and overall impacts differed between aquatic invasive species and respective native analogues, using two globally-established invasive species. We utilised the aforementioned trio of metrics (i.e. FR, FRR and RIP) to quantify the predatory impacts of two aquatic invasive species – the marine European green crab (*Carcinus maenas*) (hereafter, green crab) and the freshwater brown trout (*Salmo trutta*) – each of which are established in Canada and other regions globally. Both are listed amongst the 100 of the worst invasive species (Lowe et al. 2000), in part due to their strong observed effects on recipient ecosystems. Given that differences in feeding behaviour may influence competitive ability and ecological impact in the field (Dick et al. 2017a), we expected that the outcomes of these experiments would reflect the relative impact of both invasive and native predators.

To accurately direct management efforts of invasive species, researchers must understand their projected effect across and within regions to which the species has spread, relative to native analogues. Such predictions provide essential information to possible management interventions of invasive species.

Methods

Collection and maintenance

Brachyuran crabs

Invasive green crab (*Carcinus maenas*) and native rock crab (*Cancer irroratus*) (N = 30 each) were collected during the summer of 2015 using Fukui traps (baited with herring) from the upper subtidal zone at North Harbour within Placentia Bay, Newfoundland (NL). Green crab was first detected in this region in 2007 (Blakeslee et al. 2010) and has since spread throughout Placentia Bay and Fortune Bay on the NL south coast. In this and other regions, green crab has precipitated cascading, ecosystem-level changes to fish communities and their habitat (Matheson et al. 2016) and has had demonstrable negative effects on indigenous decapods (MacDonald et al. 2007; Rayner and McGaw 2019). Rock crab was selected given that it shares similar habitat and diet with the invasive green crab (Bélair and Miron 2009; Matheson and Gagnon 2012a, b). The former is also an economically and ecologically important species and serves

as the primary prey for American lobster (*Homarus americanus*) (Sainte-Marie and Chabot 2002).

Only male crabs with all appendages intact were selected to avoid potential variation in foraging that could result from morphological or behavioural differences between the sexes (Elner and Hughes 1978; Abello et al. 1994). We also selected only green crab with a green carapace and did not retain those with a slightly orange or red carapace, which can indicate a stronger and thicker carapace and potentially stronger chelae (Reid et al. 1997). Lastly, all crabs were hard-shelled to minimise potential foraging variation that could result from the use of individuals undergoing moulting.

Mytilus sp. mussel prey (25 ± 3 mm) – on which both crab species are known to feed (Matheson and Gagnon 2012a) – were collected by hand by divers within Conception Bay, NL. This size of mussels was selected based on previous size selection experiments with rock and green crabs (Matheson and Gagnon 2012a). Understanding the impact on mussel prey is important, given the threat posed by green crab to large-scale commercial shell-fisheries (Grosholz et al. 2011), including that of the blue mussel (*Mytilus edulis*) (DFO 2011; Pickering and Quijón 2011).

Crabs and mussels were transported in containers with seawater to the Northwest Atlantic Fisheries Centre in St. John's, NL. Species were held separately in holding tanks (275 l) equipped with a flow-through seawater system (11.8 ± 1.5 °C) and fed *ad libitum* mussels and scallops. The photoperiod (13 h light:11 h dark) was kept constant throughout the experiment. Crabs and mussels were allowed to acclimatise to the system and monitored at least one week prior to and post use in FR trials.

Rock crabs were significantly larger [carapace width (notch to notch) ± SE: rock crab: 104.3 ± 1.57 mm; green crab: 64.2 ± 0.62 mm] and heavier (mass: rock crab: 201.4 ± 7.55 g; green crab: *82.8* ± 2.45 g) than green crab (Wilcoxon rank sum: $W = 0$, $P < 0.0001$). Cheliped size, which can be a proxy for crushing strength, for the rock crab was also larger (22.9 ± 0.36 mm) than the green crab crusher cheliped (19.1 ± 0.37 mm) (Wilcoxon rank sum: $W = 81$, $P < 0.0001$). This difference resulted from the intentional selection of typical full-sized adult rock and green crabs found in the same habitats, which further allowed comparisons with other studies that used the same approach. Use of both invasive and native adult crabs, therefore, permitted us to discern maximum potential impact of these species.

Salmonids

Experimental trials with invasive brown trout (*Salmo trutta*) (N = 31: mean ± SE wet weight: 49.4 ± 2.1 g) and native Atlantic salmon (*Salmo salar*) (N = 18: 91.7 ± 5.4 g) were conducted at the University of Windsor's Freshwater Restoration Ecology Centre (FREC, LaSalle, ON Canada). Brown trout were purchased from Kolapore Springs Fish Hatchery (Thornbury, ON, Canada) in the summer of 2015 and transported to FREC in insulated tanks with continuously aerated water. Atlantic salmon were reared at FREC.

We selected brown trout as our focal invader given its cosmopolitan distribution and long invasion history (Klemetsen et al. 2003). Its ecological impacts span multiple trophic levels (reviewed in Well et al. 2017) and affect various ecosystem processes (Townsend and Simon 2006). The species has been deliberately introduced into many regions, including New Zealand (Townsend and Simon 2006) and sub-Saharan Africa (Weyl et al. 2017). However, despite brown trout's ubiquity, impact assessments in invaded habitats are relatively recent (McIntosh et al. 2011). Atlantic salmon was chosen based on its high niche overlap with our focal invader (Armstrong et al. 2003).

All fish were acclimatised for one week during which time they were fed mealworms (*Tenebrio molitor*) *ad libitum*. Animals were housed in climate-controlled facilities prior to and during experiments (15–17 °C air temperature; 10 h light:14 h dark regime). Fish from individual species were held communally in recirculating housing tanks (800 l; 5% turnover per day), in accordance with University of Windsor's Animal Care guidelines.

Experimental trials

Brachyuran crabs

FR trials were run across six circular opaque fibre-glass tanks (275 l; 100 cm diameter and ~ 50 cm water depth) configured in rows of two. Each tank was set up with its own individual light source and inflow to standardise environmental conditions (10.25 °C ± 0.04; ~ 5–10 l/minute flow rate). All tanks were covered with mesh (1.3 cm opening) to prevent potential escape. A random number generator allotted predators and prey density treatments to individual trial tanks.

Trials were conducted between 7am and 3pm. Individual crabs were selected at random and held in experimental tanks supplied with flow-through seawater 48 hours prior to experimental trial to acclimatise and standardise hunger. To initiate a trial, mussels (free of epibionts) were presented haphazardly throughout the tank at six densities (2, 4, 8, 16, 32 and 64 mussels per tank). Each feeding trial lasted five hours, after which we examined prey capture, defined as any crab-mussel interaction that resulted in the crushing or opening the shells of a mussel. We conducted five replicates at each prey density and one control trial for each prey density in the absence of a predator to quantify background mortality rates. Each crab was only used once. We excluded any trial in which the foraging crab moulted in the week following the experiment to further minimise potential variation in crab behaviour during the feeding trial.

Fisheries and Oceans Canada provided regional abundance estimates (CPUE ± SE) for both green and rock crab in North Harbour, Placentia Bay, NL. An average multi-year estimate (2015–2019) was used to account for spatiotemporal variability in population densities. Each yearly estimate was based on 12 traps (four lines of three traps set perpendicular to the shore in the shallow subtidal) set during each of five monthly surveys (June through to October). Trapping estimates recorded the number of crabs obtained per trap per day. The soak time during each deployment was approximately 24 hours with traps set at low tide.

Salmonids

Fish were starved for 24 hours to standardise hunger levels and acclimatised to experimental tanks prior to trial onset. Fish were randomly selected and assigned to one of two flow-through 50 l trial tanks (Mean ± SE: 10.24 °C ± 0.16, flow rate: 1 l/ minute) containing aquarium water. Species were alternated between trials. Tanks were wrapped in black plastic to mitigate observer influences.

To initiate the start of a trial, mealworms (1 cm, cut using a razor) were introduced to the water surface at one of six prey densities (8, 16, 32, 64, 128 and 175 prey per tank). Due to limited stock of Atlantic salmon, three repetitions were conducted per prey density with no re-use. Five replicates were performed per density for brown trout, with the exception of the prey density of 175, for which six replicates were conducted. Mealworms were launched via a weigh boat from the same point across trials. In this regard, they mimicked drifting invertebrates on which salmonids commonly feed (Bridcut 2000). Following their addition, predators were left to feed for one hour, after which they were removed and we counted the number of prey items remaining. Each predator was only used once. After each trial, we euthanised fish via MS222 (300 mg l^{-1}) and recorded their wet weight. We verified the number of prey items consumed via stomach contents. The use of dried prey precluded use of control trials for prey mortality.

To compute an estimate of the relative impact for our study species, we procured abundance estimates for Atlantic salmon and brown trout within the Credit River watershed (2015–2019) from Credit Valley Conservation Authority. The Credit River watershed is an important system for juvenile salmonids, including Atlantic salmon, of which both naturally and hatchery-reared individuals are present. Atlantic salmon is native to this region and is currently the subject of restoration efforts (Dimond and Smitka 2005). Alongside other non-indigenous salmonids, brown trout has been introduced extensively in this region to meet recreational demand (Stewart and Schaner 2002). Both species are subject to stocking (Ontario Ministry of Natural Resources and Forestry 2016).

Abundance data were obtained using single pass electrofishing [see Credit Valley Conservation Authority (2019) for a detailed overview of their methodology]. Abundance estimates were procured in the summer, several months after stocking. Estimates were calculated as the number of individual fish divided by stream area (m^2).

Statistical analyses

Data analyses were performed in R, version 4.0.2 (R Core Team 2020). Data exploration was performed according to Zuur et al. (2010). We verified the appropriateness of GLMs by visually inspecting residuals (package DHARMa, Hartig 2020).

Brachyuran crabs

We tested for effects of species (factor, two levels), prey density (factor, six levels) and their interaction on consumption rate (continuous) using a GLM (glmmTMB,

Brooks et al. 2017) with a negative binomial error distribution with default parameterisation. Crusher cheliped size (continuous) was included as a covariate in the GLM to control for its effects. A negative binomial distribution was selected after fitting candidate distributions to consumption data via maximum likelihood estimation to determine best fit (fitdistrplus, Delignette-Muller and Dutang 2015). We included a dispersion formula for prey density in the GLM to account for heteroscedasticity. Candidate models (with or without an interaction term between factors) were assessed based on Akaike's Information Criterion (AIC) and interpretation of scaled residuals. Model assumptions were verified by plotting residuals versus fitted values and inspecting residuals for goodness-of-fit patterns. We computed coefficients of the best fitting model with analysis of deviance Type III sums of squares, given the presence of the interaction term (car, Fox and Weisberg 2019). Where a term was significant, we used Tukey comparisons via estimated marginal means for pairwise testing (emmeans, Lenth 2020).

We assessed differences in *per capita* feeding rates via FR curves. We fitted both Type II and III FR models to consumption rate data, using maximum likelihood estimation (bbmle, Bolker and R Development Core Team 2016) and compared fit via AIC. To account for prey depletion over the duration of the experiment, we modelled the resultant Type II FRs using Rogers' random predator equation (Rogers 1972):

$$N_e = N_0 (1 - exp (a (N_e h - T))) \quad \text{(Eqn. 1)}$$

where N_e is the number of prey eaten, N_0 is the initial density of prey, a is attack constant, h is handling time and T is the total experimental period (5 hours).

Predator consumption rates – as well as consumer-resource interaction variables, such as search rate, detection distance and handling time on which such rates depend – often vary with individual mass (Kalinkat et al. 2013). In turn, this may implicate changes in *per capita* interaction strength between predators and their prey and the resultant FR. To account for size discrepancies between crabs, FR parameters were allometrically scaled following Kalinkat et al. (2013). We used a fixed allometric-scaling exponent of 0.65 to account for body mass-metabolic rate scaling in brachyuran crabs (Griffen and Sipos 2018), such that attack rate scaled positively with predator body mass:

$$a = a_0 m^{0.65} \quad \text{(Eqn. 2)}$$

and handling time scaled negatively with predator body mass:

$$h = h_0 m^{-0.65} \quad \text{(Eqn. 3)}$$

In both Eqns. 2 and 3, a_0 and h_0 are constants and m is predator mass (g).

We fitted the allometrically-scaled FR models using all data for a given species to obtain initial parameter estimates for bootstrapping. We then bootstrapped ($N = 100$) the data to construct 95% confidence intervals around the fitted curves and extract

median values for model parameters. Convergence in FR confidence intervals indicated a lack of significant difference between species' consumption rates.

We computed FRRs (attack rate *a* divided by handling time *h*, i.e. *a/h*) for each species using median attack rate and handling time parameters. The FRR is a novel metric that has successfully differentiated ecologically-damaging invasive species (Cuthbert et al. 2019). Higher values indicate greater inferred impact, since high values of *a* and low values of *h* both predict high *per capita* effects across the FR curve and, hence, across low and high prey densities (Cuthbert et al. 2019).

Finally, we determined the maximum feeding rate of each predator (*1/h*) and combined these values with field abundance estimates to derive a Relative Impact Potential (RIP) estimate according to Dick et al. (2017a):

$$RIP = \left(\frac{\text{FRinvader}}{\text{FRnative}} \right) * \left(\frac{\text{ABinvader}}{\text{ABnative}} \right)$$

This allowed us to discern the relative impact of introduced green crab to native rock crab.

Salmonids

Using the same methodology as described above, differences in overall prey consumption amongst species (factor, two levels), prey density (factor, six levels) and wet weight (continuous) were assessed using a GLM with negative binomial error distribution (glmmTMB, Brooks et al. 2017). As there was no interaction found between the main factors, interaction terms were removed to identify the most parsimonious model. We incorporated a dispersion model to account for heteroscedasticity amongst prey densities and between species. We used Type II analysis of deviance to compute overall effects of GLMs (car, Fox and Weisberg 2019) and made post-hoc pairwise comparisons using Tukey's tests [package emmeans (Lenth 2020)].

FR type was confirmed following the protocol outlined above. We subsequently incorporated allometric functions in FR models to account for size discrepancies between salmonids (Kalinkat et al. 2013). On average, metabolic rates in fish conform to a 0.89 power-law scaling of maximum consumption with predator body mass (Jerde et al. 2019). Handling time and attack rate parameters were scaled negatively and positively, respectively, using a fixed allometric exponent of 0.89.

Allometrically-scaled FR models were fitted following the aforementioned methodology to obtain median estimates of attack rate and handling time. We then computed FRRs (*a/h*) for each species as well as corresponding maximum feeding rates (*1/h*). We subsequently used both species' maximum feeding rates and abundances to compute the RIP estimate. Stocking effort and abundance were both greater for the native Atlantic salmon. Given field abundance disparities between our focal salmonid predators, we projected impact potential of brown trout in increments of 0.01 ind/m^2 to determine the point at which RIP would exceed a value of 1. That is, we determined when brown trout's projected ecological impact may exceed that of native Atlantic salmon.

Results

Brachyuran crabs

In control trials, we experienced no prey mortality and thus ascribed all prey death to predation, which was also directly observed. Predator consumption rates were best described by Type II FRs (Fig. 1).

On average, rock crabs consumed more mussels than green crabs, though the difference was not significant (Wilcoxon: W = 415, P = 0.61). Analysis of species' *per capita* effects revealed more nuanced differences in consumptive impact. Rock crab consumed more mussels than green crab, both with and without correcting for size differences between crab species (Table 1; Suppl. material 1: Table S1). Differences in consumption rates between species was contingent on prey density (species * prey density: $\chi^2 = 29.04$, df = 5, P < 0.0001). Rock crabs out-consumed their invasive analogues at higher prey densities (32 prey: estimate ± SE: -0.80 ± 0.24, P = 0.002; 64 prey: -0.44 ± 0.25, P = 0.09) (Fig. 1). However, species' consumption rates were not significantly different at low prey densities, as evidenced by overlapping confidence intervals (Fig. 1). Cheliped size – here used as a proxy for crushing strength – was significantly and positively associated with consumption rate ($\chi^2 = 6.28$, df = 1, P = 0.01).

Green crab had a higher FRR, reflecting a steeper FR curve at low prey densities (i.e. larger attack rate, *a*) that compensated for a higher handling time (*h*; and, hence, lower maximum feeding rate), indicating European green crab will potentially impact prey populations more than rock crab. Further, green crab abundance (mean ± *SE*: 29.44 ± 6.91) was orders of magnitude greater than that of rock crab (0.17 ± 0.12), driving a large RIP value (Table 1, Fig. 2).

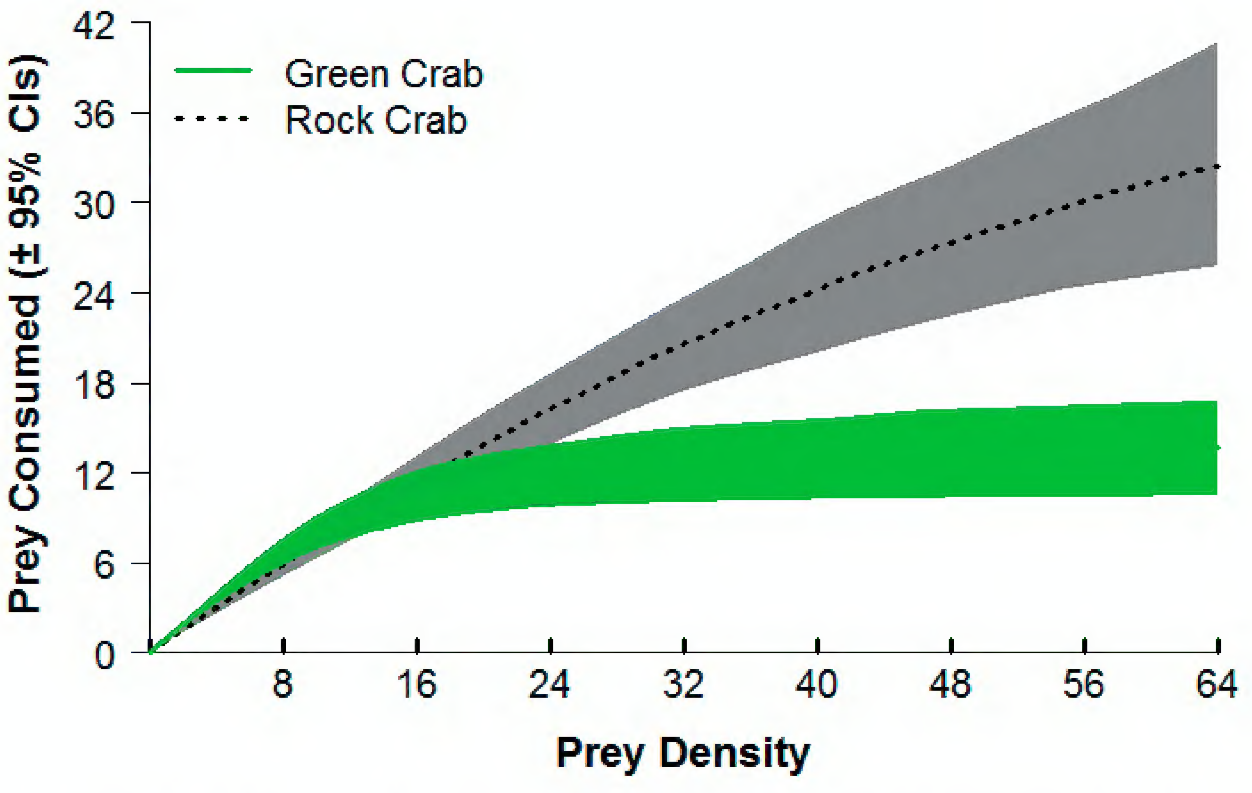

Figure 1. Functional responses of invasive green crab and native rock crab towards mussel prey. Lines represent initial functional response fits from the random predator equation; shaded areas are 95% confidence intervals (n = 100 non-parametric bootstraps).

Table 1. Relative Impact Potential (RIP) and Functional Response Ratio (FRR) scores, as well as mean ± standard error (SE) estimates of maximum feeding rate, recorded for both invasive-native species pairs. RIP > 1 are predicted to be high impact invaders, those < 1 are low impact relative to native predators.

System	Species	Maximum feeding rate (*1/h*) (± SE)	RIP	FRR (*a/h*) (± SE)
Marine	Green crab	0.82 (0.01)	71	0.17 (0.01)
	Rock crab	2.02 (0.19)		0.12 (0.01)
Freshwater	Brown trout	0.48 (0.01)	0.20	0.04 (0.002)
	Atlantic salmon	0.41 (0.02)		0.001 (<0.001)

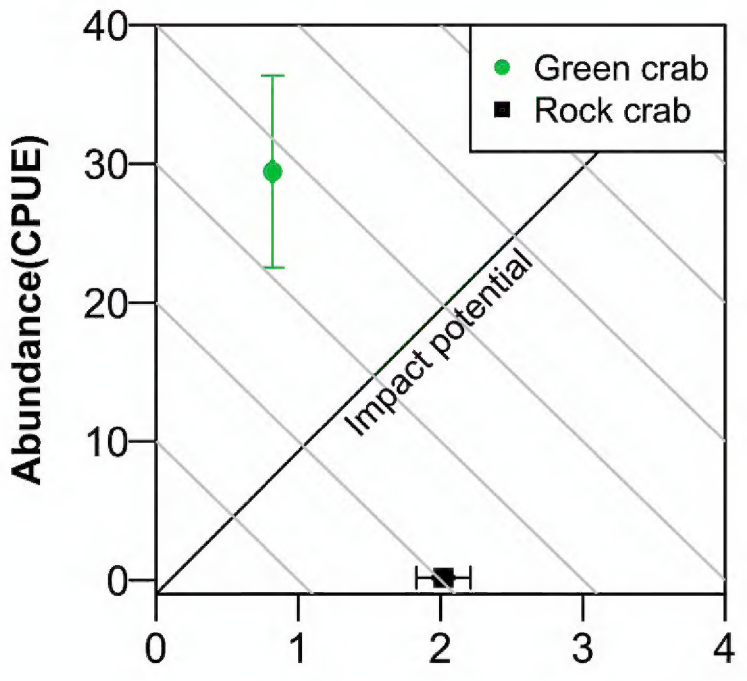

Figure 2. RIP biplot comparing invasive green crab and rock crab feeding upon native mussel prey. Biplots generated using mean ± standard error (SE) estimates for FRs (allometrically-scaled maximum feeding rate, prey/5 hour) and field abundances (CPUE). Ecological impact increases from bottom left to top right.

These results corroborate two independent Ecological Impact Scores used by Laverty et al. (2015) and Ricciardi and Cohen (2007). Both Scores are ordinal rankings of impact, where higher scores demonstrate more negative effects. Maximum available scores for each metric are 5 and 7, respectively. Using the regression equations in Figure 2 of Dick et al. (2017a) – the relationship between actual field impact and RIP value – we predict green crab to have serious ecological impacts of 4.05 on the Laverty et al. (2015) scale and 6.05 on the Ricciardi and Cohen (2007) scale.

Salmonids

Both salmonids exhibited Type II FRs (Fig. 3). While Atlantic salmon was significantly heavier than brown trout (Wilcoxon: $W = 528.5$, $P < 0.0001$), the latter, on average, consumed significantly more prey both in terms of raw consumption and per unit mass (raw: Wilcoxon: $W = 117$, $P = 0.001$; per unit mass: Wilcoxon: $W = 74$, $P < 0.0001$).

Consumption rates increased significantly with increasing prey density ($\chi^2 = 32.40$, $df = 5$, $P < 0.0001$) and by predator mass ($\chi^2 = 16.60$, $df = 1$, $P < 0.0001$). Brown trout was more voracious than Atlantic salmon across all levels of prey availability ($\chi^2 = 46.17$, $df = 1$, $P < 0.0001$) (Fig. 3). However, consumption rates were not significantly

different at the highest two prey densities, as evidenced by overlapping confidence intervals. The observed FR relationship was unchanged when correcting for size differences between salmonids (Table 1; Suppl. material 1: Table S1).

Brown trout exhibited a higher maximum feeding rate and FRR relative to Atlantic salmon (Table 1). However, their lower field abundance dampened the resultant RIP (Table 1, Fig. 4). Modelling of projected impact potential suggests that an

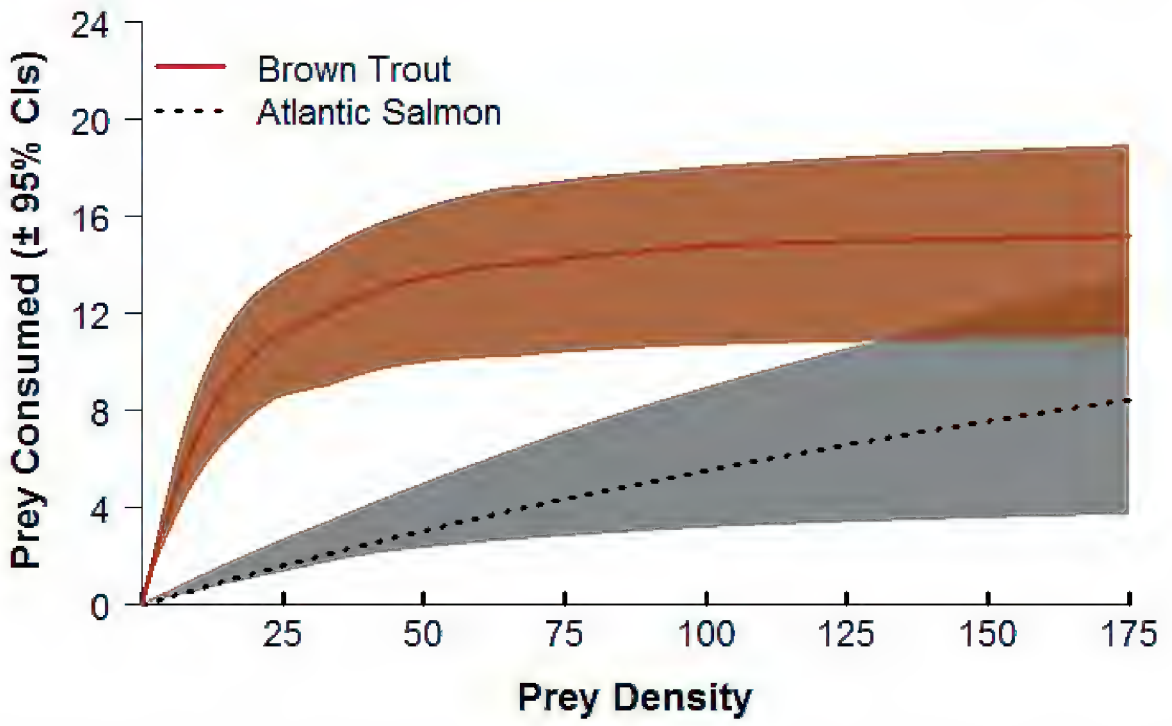

Figure 3. Functional responses of invasive brown trout and native Atlantic salmon towards dried mealworm prey. Lines represent initial functional response fits from the random predator equation; shaded areas are 95% confidence intervals (n = 100 non-parametric bootstraps).

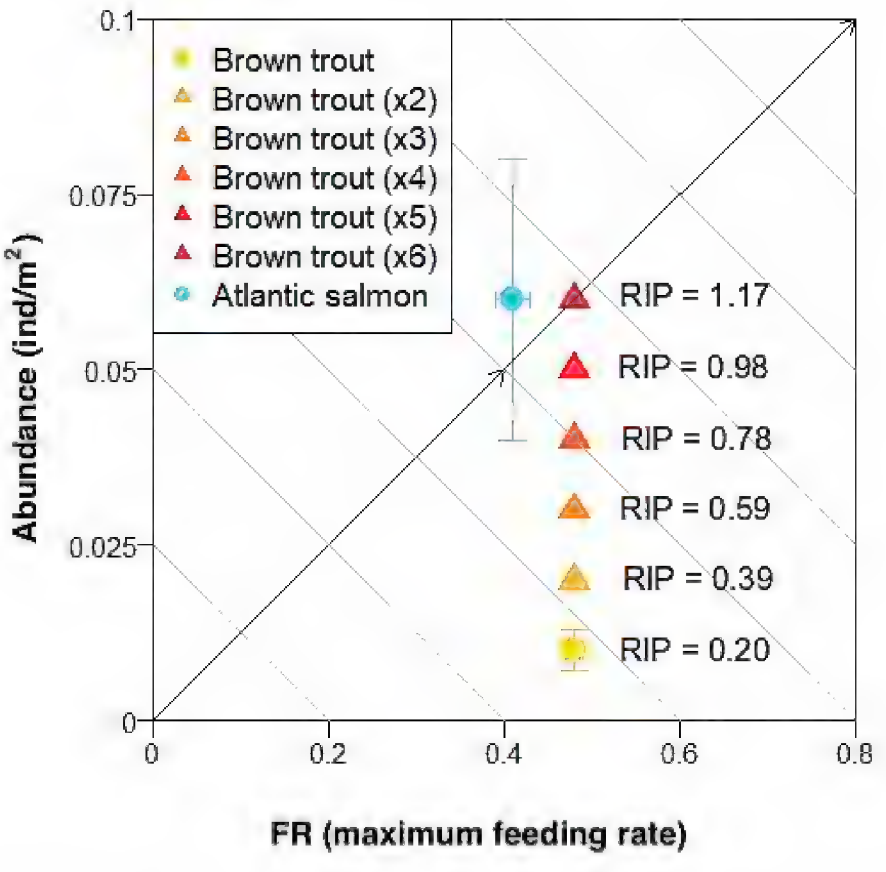

Figure 4. RIP biplot comparing invasive brown trout and Atlantic salmon feeding upon mealworm prey. Biplots generated using mean ± standard error (SE) estimates for FRs (allometrically-scaled maximum feeding rate, prey/hour) and field abundances (ind/m^2). Ecological impact increases from bottom left to top right.

abundance of 0.06 ind/m^2 – equivalent to that of Atlantic salmon – would be required to increase the RIP to a level where brown trout would exert a greater impact than Atlantic salmon (Fig. 4).

Discussion

Understanding differences in resource consumption by invasive and native species can provide meaningful insights into potential impacts of invaders in colonised ranges (Dick et al. 2014). When combined with an invasive species' abundance, meaningful understanding of expected ecological impacts may become apparent (Dick et al. 2017a; Ricciardi et al. 2021). Here, we examined *per capita* effects of two notorious invasive species using functional response (FR) methodology and the new Functional Response Ratio (FRR) and, subsequently, examined how these effects were modified by each species' abundance using the Relative Impact Potential (RIP). This combined experimental approach links *per capita* feeding rate with field abundance to provide best estimates of invader impact relative to comparable native species (Dick et al. 2017a; DeRoy et al. 2020).

Our study highlights strong density-dependence of both *per capita* and total estimated population effects. All species demonstrated inverse density-dependent prey mortality and potentially destabilising Type II FRs for prey populations. While invasive species often exhibit higher FR curves relative to functionally analogous native species (Dick et al. 2014), we observed mixed results. FR results suggested a strong *per capita* effect by brown trout and a much more muted one by green crabs, relative to their native analogues. However, the FRR metric, which blends the parameters of attack rate (a) and handling time (h), was a good predictor of both invasive species having high impact on native prey compared to that of native predators (see Cuthbert et al. 2019). Relative impact incorporating species' numerical responses better captured the full potential of each invader and suggested dominant impacts overall by each of green crab and Atlantic salmon. We expect differences in projected impact reported herein to correlate with field ecological impacts, as corroborated by past research (Dick et al. 2014; Dick et al. 2017a).

Invasive species' impacts are often context-dependent, in part mediated by abundance (but also *per capita* differences; see Howard et al. 2018). Reported abundance of green crab in Placentia Bay exceeds that of the species elsewhere in the Canada's eastern provinces (DFO 2011) as well as in western United States and Canada (Yamada et al. 2020; Ens et al. 2021). Such differences may portend dissimilar ecological impacts. Their high population abundance also highlights potential commercial impacts on bivalve and lobster fisheries. Aquaculture is a growing economic driver for many locations, such as the Atlantic Canadian region, which is highly dependent on eastern oyster (*Crassostrea virginica*) production (Bernier et al. 2020). Actual and potential fisheries impacts of green crab have been well-documented throughout their invaded range (Yamada 2001; Matheson and McKenzie 2014; Rayner and McGaw 2019),

with economic losses projected to increase with their range expansion (Grosholz et al. 2011). Such inter-regional differences in ecological and economic impact of green crab need further exploration globally.

The high attack rate of green crab at low prey densities can potentially drive mutual prey species to become increasingly rare or even extinct (Dick et al. 2014) (Fig. 1). These impacts on native prey populations could have negative spill-over implications for native rock crab. Green crab's abundance, in conjunction with their high attack rate, could exclude rock crab from preferred resources like mussels. However, species' prey consumption suggests that rock crab could co-exist with green crab in areas where the latter is present at low abundance or when prey abundance is sufficiently high. As a result, where green crab numbers are high, species' co-existence could be facilitated by numerical control of the invader. However, traditional population suppression is complicated by the life history of green crabs, which demonstrate the potential for density-dependent, stage-specific overcompensation (Grosholz et al. 2021). That is, eradication efforts targeting adult green crabs may inadvertently facilitate enhanced survival and growth of juveniles released from cannibalism (Grosholz et al. 2021). To protect against such a scenario, functional eradication – suppressing populations below the threshold that would cause significant ecological harm and a positive numerical response by juveniles – may prove viable (Green and Grosholz 2021). Findings, presented herein, may provide a useful starting point to understand the species' non-linear population dynamics, on which the aforementioned management strategy is based.

Analysis of freshwater salmonids revealed greater levels of consumption by brown trout across all levels of prey availability, despite their smaller size. These findings are consistent with FRs of other high impact invasive species (Dick et al. 2014) and are in accordance with strong negative effects of brown trout in invaded systems (reviewed in McIntosh et al. 2011). Effects of brown trout may be most significant under resource limitation owing to their high FR and heightened attack rate at low prey densities.

Field abundance provides an estimate or proxy of predator numerical response (Dickey et al. 2020a and 2021) and, when combined with FR data, extends predictive understanding of ecological impacts substantially (Dick et al. 2017a). Widespread stocking of brown trout has traditionally supported its range expansion, often at the expense of native fishes (McKenna Jr et al. 2013). Despite high reported abundances of brown trout throughout its introduced range (for example, in excess of 1 ind/m^2, McIntosh et al. 2011) – which frequently exceeds that of sympatric natives (Jones and Closs 2011; Al-Chokhachy et al. 2016) – native Atlantic salmon is purported to have a greater ecological impact on prey within the sampled watershed as a consequence of its high relative abundance (Fig. 4). These disparities in abundance are similar elsewhere regionally where the species are sympatric (Larocque et al. 2020).

Abundance discrepancies may dampen the potential for interspecific competition and produce limited, but strong interactions between the two species, as evidenced by their overlapping isotopic niches (Larocque et al. 2020). Furthermore, resource partitioning between Atlantic salmon and resident fish appears to reduce trophic interactions (Larocque et al. 2020), which may further species' co-existence. These results

support the need to disentangle density-mediated effects from *per capita* effects to better understand the processes driving impacts of individual invasive species.

The current risk of brown trout appears low, based on analyses of population-level impact. However, numerical estimates of abundance, as reported herein, may not represent abundances of the focal species in other systems. It is possible that brown trout impact could be far more substantial in areas where the numerical difference between these species is lower (and in systems without external manipulation), as corroborated by our model (Fig. 4).

Our findings have important implications. If left unchecked, they suggest that burgeoning brown trout populations are likely to produce significant ecological impacts, potentially to the detriment of both native Atlantic salmon and prey populations. Despite the invader's high *per capita* effect, management interventions can suppress its potential population-level impact on recipient systems by keeping relative densities low. Sustaining native species' populations while ensuring productive fisheries – like that of brown trout – therefore depends on balanced management (Dettmers et al. 2012). It also suggests a need to reconcile the paradox of brown trout as both an important sport fish and a detrimental invader (Cowx et al. 2010).

Future research

Future research should consider the ecological impact of our focal species across a wider variety of prey types in field and laboratory settings. A growing body of literature reinforces the resource-specific nature of invasive species' *per capita* effects (e.g. Chucholl and Chucholl 2021). We encourage subsequent studies to consider ecological impact under varying prey and resource identities to gain a more complete picture of predator-resource dynamics, as differences or similarities in prey preference and related competitive interactions can have cascading influences on overall ecological patterns and impacts.

Additionally, investigation into non-consumptive effects of both green crab and brown trout are needed to ascertain implications for native predators and ultimately consequences to prey. For example, habitat use and depth distribution overlap in shallow waters in areas where our focal crab species co-occur (Tremblay et al. 2005; Matheson and Gagnon 2012a). Green crabs are also highly agonistic and territorially competitive, often outcompeting other crustaceans in foraging and shelter contests (McDonald et al. 2001; MacDonald et al. 2007; but see Jensen et al. 2002). These factors may lead to exploitative and/or interference competition for food or habitat, which may increase as green crab become more numerically dominant. Similarly, brown trout often occupy preferred foraging positions which provide preferential access to food (Alanärä et al. 2001). Brown trout is also a better competitor relative to Atlantic salmon (Van Zwol et al. 2012) and exhibits higher levels of aggression (Scott et al. 2005; Van Zwol et al. 2012; Houde et al. 2015). These traits may hinder the growth, survival and consumption rates of native species like Atlantic salmon (Van Zwol et al. 2012; Houde et al. 2015). In turn, interactions between invasive and native predators may ultimately influence each predator's *per capita* effects on prey populations. Whether these effects

have the potential to subsequently mediate ecological impact remains unclear – and is beyond the scope of this study – but demands further investigation.

Understanding the synergistic influence of co-occurring stressors on invasive species' impacts is a priority area for invasion science (Ricciardi et al. 2021). Future changes in environmental parameters, such as temperature and salinity, have the potential to mediate feeding behaviour (Iacarella et al. 2015; Dickey et al. 2020b), as well as prey availability, and should be incorporated into subsequent impact predictions. This area of research is particularly important for aquatic invasive species, for which research investigating the combined influence of temperature and salinity regimes is scant (Cuthbert and Briski 2021). Physiological tolerances of our focal invasive predators portend increased impacts in light of a changing climate. Green crabs have broad physiological tolerance (Simonik and Henry 2014) and predation rates are positively correlated with temperature (Matheson and Gagnon 2012a, b). Increases in water temperature are similarly likely to favour brown trout at the expense of native salmonids (Al-Chokhachy et al. 2016; Hoxmeier and Dieterman 2019). The potential for variations and potentially higher impact under climate change thus warrants additional studies across taxonomic groups.

Conclusions

Functional and numerical response methodology provides meaningful insights into assessing invader impact and has become especially robust when used in conjunction with the FRR and RIP metrics. These results imply that, if the *per capita* impacts and relative abundance of non-indigenous species are well-known, its potential relative impact can be predicted and appropriate management actions devised, if needed. Our findings further underscore the importance of population suppression to effectively manage invasive species and promote co-existence with native analogues and prey populations. While our results provide novel insights into the implications of our focal predators, further work is required that incorporates environmental change scenarios.

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Supplementary material 1

Table S1

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Data type: docx file

Explanation note: Unscaled mean ± standard error (SE) estimates of maximum feeding rate and Functional Response Ratio (FRR) scores, recorded for both invasive-native species pairs.

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